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BULLETIN

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Antidromy of Plants.*

By George Macloskie.

During the summer of 1893 I made observations on Indian corn, which were published in abstract in the Princeton College Bulletin of November, 1893. It was then shown that, if we judge from the modes of overlapping of the leaf margins of Maize and of other Gramineae, there must be two kinds of plants of every species of the order; the one kind or "caste" has its lowest foliage leaf (the leaf next above the pileolus in the embryo) with the right margin of its sheath overlapping the left margin, "dextrally infolded" as I term it; and the other caste has the left margin overlapping the right, "sinistrally infolded." The leaves at subsequent nodes are alternately sinistral and dextral. In order to ascertain the origin of this duplicity I read Van Tieghem's researches on the Cotyledons of the Gramineae (Ann. des Sci. Naturelles, 1872), which stated that the leaves of the plumule within the seed are alternately enfolded on each other, but failed to indicate the direction of the enfolding of the first leaf.† The dissection of one or two seeds revealed a dextral initial folding; and soon other grains were found with sinistral folding. Thus it became manifest that as there are two castes of maize-plant, so

* Read before Section G., A. A. A. S., Springfield meeting, September, 1895.

† He states that the direction of the evolution of the leaves is determinate, but there is variation as to the first green leaf, and he had not been able to discover its cause.

there are two castes of grains, the one being the "anudrom" of the other, the leaf-folding starting diversely, and the leaves of successive nodes, running contrariwise in the plumule of one grain as compared with that of another grain.

The next problem was to orientate the grains of each caste in the ear of Maize. The ear consists of columns each containing a pair of rows of grains; we may designate the row opposite our right hand dextral and the other row (opposite our left) as sinistral. It was soon made out that in the particular ear examined, the grains of the dextral row were all with dextral embryos, and those of the sinistral row had sinistral embryos. Whether this law would apply to all the ears on one plant, or whether the order would be inverted between the ears arising from successive nodes, or between the ears of different plants, is yet to be determined. On examining the very young ear of maize I found the grains of the paired rows of each column orientated close to each other, almost face to face, the young styles running up together, and a gap between the adjoining two-rowed columns.

From this discovery the inference was obvious that the seeds of corn differ from each other antidromically, according to the side of the placenta or axis from which they arise; that their embryos vary in consequenee, and determine the caste of the future plant. Whilst it was easy to see that the same rule will include all the Gramineae, I hazarded the suggestion that it may be found in some measure to dominate other orders of plants. The discovery as to the corn disposes of Sachs's crowning argument against phyllotaxy, which he supposed could have no significancy as to Gramineae, on account of their distichous leaves.

Early in August, 1895, I was struck by the graceful inflorescence of Ladies' Tresses (*Spiranthes praecox* Watson, *S. graminea* var. *Walteri* Gray). Its spiral rows of pure white flowers are antidromic as between different individual plants; about half the specimens have dextral spirals (viz., turning in the direction of the thread of a common screw), and the same number have sinistral spirals. Another interesting point was that the phyllotaxy, or arrangement of the distichous leaves in a primitive spiral, of each of the plants of *Sptranthes* follows the order of the inflorescence, dextrorse phyllotaxy invariably accompanying the dextrorse an-

thotaxy, and conversely.* The numerous seeds of these plants are too small to be easily compared together; but the phyllotaxy or even the inflorescence serves as our best guide when other indications fail. A similar remark will apply to *Oenothera biennis*, whose inflorescence curves to the right or left in the same direction as the leaves; though not always so easily determined as in Ladies' Tresses. In some cases the seeds form a ready guide. For example, the Lima-bean is found on examination to have its cotyledons right and left, and two foliage leaves respectively dorsal and ventral (towards the dorsal and ventral sutures of the pod). Now I found that the right margin of the dorsal leaf of the plumule of one seed overlaps the right margin of the ventral leaf, but the left margin of the dorsal leaf is overlapped by the left margin of the ventral leaf; and in another seed these relations are reversed. I also found that the seeds growing on one valve of the pod, being Nos. 1, 3, 5, were all similar; whilst the seeds on the other valve, being Nos. 2, 4, were reversed. Thus the seeds on one margin of a carpel are found to be antidromically related to those on the opposite margin. (I have not examined whether successive pods from the same plant reverse these characters or not.) The pea showed its antidromy best when germinating, the emerging plumules of different seeds appearing under careful orientation to come up with opposing twists. The large plumule of the Almond seed can be seen by dissection to have two modes of torsion in different seeds. The akenes of *Caffea* exhibit antidromy, an interesting point in this plant as the opposite leaves render the determination otherwise difficult. The deeply enfolded endosperm of the coffee-bean is seen on a cross-section of different seeds to be in opposite directions; a mark which is a sure indication of similar diversity in the minute embryo. Even from the outside the two kinds of akenes are easily distinguishable, the figure of one reversing that of the other like one's right and left hand, thus proving that the two mericarps are relatively antidromic; and confirming the evidence already derived from the corn and Lima-bean, as to the origin of this character.

* Dextral phyllotaxy has the primary spiral traced by the insertion of the leaves directed like the thread of a common screw. With leaves overlapping at the margins, dextral overlapping may produce sinistral phyllotaxy.

The case of *Banksia* of Proteaceae further illustrates the subject. Judging from the figure in Engler and Prantl's Pflanzenfamilien, (3 : part 1, 152) it has a pair of flowers, situated back to back, with bractlets, stamens, ovary and seeds, all antidromic; in this case the diversity of the seeds seems to be anticipated by the structure of the flower. The flowers on the same branch of *Althaea* have their petals twisted in contrary directions.

In connection with the explanation of antidromy as depending on the origin of seeds along the margins of a bilateral organ, it would be interesting to examine the few cases in which seeds are represented as terminal on the floral axis, a view which may be confirmed or refuted by this law. It is likewise interesting to note that in specimens of *Bryophyllum calycinum* (kindly furnished me by Prof. S. T. Maynard, of Amherst Agricultural College), I was able in this opposite-leaved flower to make out the marginal buds on the leaves to be antidromous. The Calla lily (*Richardia*) has both the alabaster spathe and the arrangement of the akenes on the spadix antidromic as between plants which grow from the same rootstock. The Iris also when growing by bifurcation of the rootstalk gives antidromic plants; how they are when propagated by lateral branching I cannot say. Rushes growing together in clumps are antidromic as between the individuals united at the base of the rootstalk (I do not find it so in *Carex* or grasses growing in tufts; all of the same tuft seem to me to be homodromic, but this subject requires more careful examination than I have made).

Phyllotaxy is a particular outcome of antidromy, and in very many cases is the readiest evidence of the antidromic organization of the plant. But whilst antidromy is a primitive character, influencing the general morphology of the plant, yet each part of the evidence, and most frequently the order of the leaves, the inflorescence and the perianth, may be modified by secondary changes, which send us back to the mother-seed and its germination as the only remaining proof of the primitive character. Twining of stems, contortion of perianth, accumulations of flowers in complex ramifications, leaves becoming opposite, or being spread out to the sunlight, and even difficulties of orientation of seeds disguise the truth and explain why it has so long remained a

secret. The distortions of phyllotaxy misled the early students on the subject, so as to nearly banish the term and the theme from botanical science. Old books spoke vaguely of some plants being *homodromous* and others *heterodromous*, without attempting to find any law to explain these apparent irregularities. We now see its significancy and find its anomalies all reduced to order, and we must welcome it back to its rightful place. So far as I have been able to find, all plants are homodromic within the individual, and heterodromic as between different individuals of the same species. Apparent exceptions to these rules are no more than apparent, and if anybody will set himself to look up the evidence, it will soon be so overwhelming, and nothing against it, as to render his work monotonous. Go into the nearest orchard and you will find two kinds of every species of fruit tree, two kinds of every shrub, two kinds of common flowers, having the primary spirals of the leaf-insertions dextral in one set and sinistral in the other set. In case of plants with opposite leaves this evidence will fail you, for you can make out two crossing primary spirals in the same branch; in other cases you are baffled by the leaves assuming new positions for the sake of the light, though sometimes even in these plants you may find the primitive traits in branches not exposed to the sunlight.

With a few weeks' observation I have found double phyllotaxy, as a mark of antidromy in the following plants representing the more important orders of Phaenogams: *Delphinium* (Ranunculaceae), *Liriodendron* (Magnoliaceae), *Bocconia* (Papaveraceae), mustard (Cruciferae), *Abutilon* and *Hibiscus* (Malvaceae), *Pelargonium* and *Impatiens* (Geraniaceae), bean and pea (Leguminosae), apple, pear, peach (Rosaceae), *Oenothera* (Onagraceae), carrot (Umbelliferae), sunflower and other Compositae, *Lobelia* (Lobelieae), *Myosotis* (Borraginaceae), *Verbascum* (Scrophulariaceae), tobacco (Solanaceae), *Polygonum* (Polygonaceae), *Ricinus* (Euphorbiaceae), *Salix* (Saliaceae), *Quercus* (Cupuliferae), and among monocotyledons, lily (Liliaceae), *Musa*, Ladies' Tresses (Orchidaceae), species of Aroideae, Iridaceae, Juncaceae, Cyperaceae, Gramineae. To the above we have to add from the perianth and arrangement of stamens Nymphaeaceae; and by the courtesy of Mr. Everett H. Barney, of Springfield, Mass., I was furnished from the Forest Park Ponds

with seeds of *Nelumbium* which on being opened, showed the embryos rich in chlorophyll, with their leaves in one seed folded round in the inverse order of those in another seed; besides this the insertion of the stamens in the flower of different individuals of *Nelumbium* form antidromic spirals. A special case among the Liliaceae is *Convallaria majalis*, whose two leaves are at the usual angle among the Monocotyledones of 120°, and as one of the leaves forms a sheath around the other, it is instructive to observe how in a bed of Lily-of-the-Valley, all the plants being regarded under the same orientation, the inner leaf in half the plants bends over 120° to the right, and in the other half to the left. Arthur K. Harrison of Lebanon Springs, N. Y., informs me that before he heard of my work he had taken note of the double phyllotaxy of *Veratrum viride*.

With a little care we can make out the general law as applying to the Gymnosperms; both the phyllotaxy and the spirals of the cones of Coniferae show it; and it may be expected to manifest its presence in the relative position of the cotyledon, during germination; also in the embryo and its suspensor in *Cycas*. (See figures in Engler & Prantl, 2: 1. 17.)

I have not yet tried the opposite-leaved orders, further than the case of *Caffea*, and that of *Bryophyllum*, as insufficiently tested by the marginal buds on the leaves; if this last observation be verified, it may reinforce the old doctrine that ovules are the homologues of such marginal buds. *Acer platanoides* shows it by the antidromic folding of the cotyledons of the seeds of adjoining carpels; also *Aesculus* by the contrary curvature of its radicles and by its plumules. Nor have I tried the twiners and climbers, saving that I have partially succeeded with Morning-glory (Convolvulaceae). Its embryo resembles that of some Cruciferae in having the radicle folded "incumbently" upon the cotyledons; and again (unlike the Cruciferae) its orientation is changed so that the radicle lies next the floral axis and the cotyledons lie towards the periphery. Now if we reduce the orientation back to that of Cruciferae, we shall find a very close correspondence of the embryonic structures in the two orders, and the same antidromic difference will be found in Convolvulaceae that is readily shown by the phyllotaxy of Cruciferae.

The embryo of *Lepidium Virginicum* has its cotyledons twisted so as to be erroneously described in the books as accumbent; something similar occurs in *Sisymbrium officinale.* In these cases the adjoining seeds have the embryos twisted in contrary directions, so that the apparent anomalies are explained as cases of pronounced antidromy. Whilst the pericarp of akenes follows the torsion of the enclosed seed, capsular pericarps seem to follow the phyllotaxy of the mother plant; thus the pods of mesquit (*Prosopis*) are similarly twisted in the same plant, as are those of *Medicago*, those of balsam (*Impatiens fulva* and *I. balsamina*) spring open with a right or left twist in harmony with the dextral or sinistral phyllotaxy of the bearing plant.

Amongst the peculiar cases that occurred was that of *Salix Babylonica*, of which only the female plants are known; and consequently there is no reproduction by seed, and we expected to find no antidromy. Specimens growing about Princeton appear to be sinistral in their phyllotaxy, and as tradition derives them from the tree growing by Napoleon's grave at St. Helena the inference arises that the St. Helena willow also was sinistral. This inference is confirmed by a young tree in Forest Park, at Springfield, which Mr. Barney knows to have come from St. Helena. But other specimens of the same species with dextral phyllotaxy are common. Thus we learn that whilst all representatives of the male line of this species have probably perished, there are at least two independent branches of the female line perpetuated by cuttings.

Another interesting case is that of *Canna.* The leaves of all the specimens which I have found at Northampton, Mass., and at Princeton, are when young spirally folded, right flap uppermost, and when expanded have a slightly dextral phyllotaxy. I am told that this is usually propagated from bulbs; but that it is sometimes grown from seeds; if this last statement be true we should expect individuals of both castes; but I have been unable to find any except the one caste (even a second variety bearing reddish leaves is by coincidence of the same cast as the common one). Doubtless the other caste occurs through the country.

The scape or flower-stalk of *Canna* may cast light on the structure of Gramineae. Whilst all the foliage leaves of the *Canna*

(so far as I have seen it) are dextral, the flower-stalk is provided with a succession of sheathing bracts, the edges folding over each other in reversed order at every succeeding node. This is exactly as in Maize, being a special kind of phyllotaxy, which depends not on a primary spiral, but on a reciprocating overlapping of the margin of sheathing organs; also a double leaf between each branch and the mother-axis is present as described by Van Tieghem in Maize. Thus it appears that the whole corn-plant, culm, leaves and flowers is the counterpart of the flower-stalk of canna and of its bracts and flowers, but having no representative of its foliage-leaves. According to this view one part of the reduction of the Gramineae is the non-development of proper foliage leaves, and by way of compensation the excessive development of the bracts with a green lamina for assimilation. It is of special advantage to gregarious plants to have their assimilating organs lifted up to the air and sunshine. (No notice is taken of the peculiar alternancy of leaves of gramineae by Pax, Vines or the other recent writers on Morphology).

Among the results of this account may be mentioned the extension of unity of primitive structure thus shown to exist among all the Phaenogams; a unity that may yet be found to include some of the Cryptogams; also the relative simplicity of the Monocotyledones, which show few secondary distortions, though they are often reduced. A new problem of heredity is started, running differently through two sides of the carpel; yet each seed transmits both castes, one to appear forthwith in its immediate offspring, and the other to appear ultimately in a moiety of its successors. The objection that the discontinuity between carpel and ovule negatives the possibility of such transmission of characters is of no weight; the discontinuity is only apparent, for characters of secondary acquirement are carried across the gap, and *a fortiori* we may expect such a primitive law of organization as antidromy to be inherited. This law is also useful to suggest discovery. It suggested to me at the outset diversities between the stalks and inflorescence of Iris that had escaped Arnold Dodel in his study and illustration of *Iris Sibirica*, which was the work of some years; it has also opened problems about the significancy of opposite leaves, the real direction of leaf-traces in stem-struc-

ture (hitherto assumed to be entirely symmetrical) and other subjects bearing on vegetable anatomy, and the difficulties which brought discredit on phyllotaxy all vanish. Perhaps it may furnish a solution of the problem why wooden poles split in antidromic spirals, for which phenomenon some people have suggested the stress of wind on the living tree.

My work has been necessarily hurried; and I shall be glad if others will verify or amend it, and help to fill the many lacunae which I am compelled to leave unsupplied.

PRINCETON COLLEGE, Sept. 7, 1895.

Description of a new problematical Plant from the Lower Cretaceous of Arkansas.

BY F. H. KNOWLTON.

PALEOHILLIA ARKANSANA gen. et. sp. nov.

Stems hollow, .5–.75 cm. in diameter, several centimetres long, broken; wall two or three layers of cells thick; cells of epidermis of two kinds: 3–5 longitudinal rows of elongated, thin-walled cells that are two or three times longer than wide, alternating with broad bands of shorter and more irregular cells; stomata numerous, confined to the broad bands of irregular cells, arranged in three rows, two next to the rows of elongated cells with a row of distant ones between; stomata with apparently 4–6, usually 5, guardian cells.

The material upon which this description is based was collected by Prof. R. T. Hill, of the United States Geological Survey, during the season of 1888, while engaged under the auspices of the Arkansas Geological Survey in making a general investigation of the geology of southwestern Arkansas. It came from a gulch on one of the smaller branches of the Muddy Fork of Little River, about six miles northeast of Center Point, Howard county. The deposits containing these fossils were referred by Prof. Hill to the Trinity Division of the Lower Cretaceous. The beds are described as consisting of basal ferruginous sands, succeeded by firm white or yellow sand often filled with small concretions of iron pyrites, and mixed with clay. This clay is in sufficient quantity to bind the sandy material together "so that in drying it often becomes